Population dynamics reveal conservation priorities of the threatened New Zealand sea lion Phocarctos hookeri

Stefan Meyer, Bruce C. Robertson,
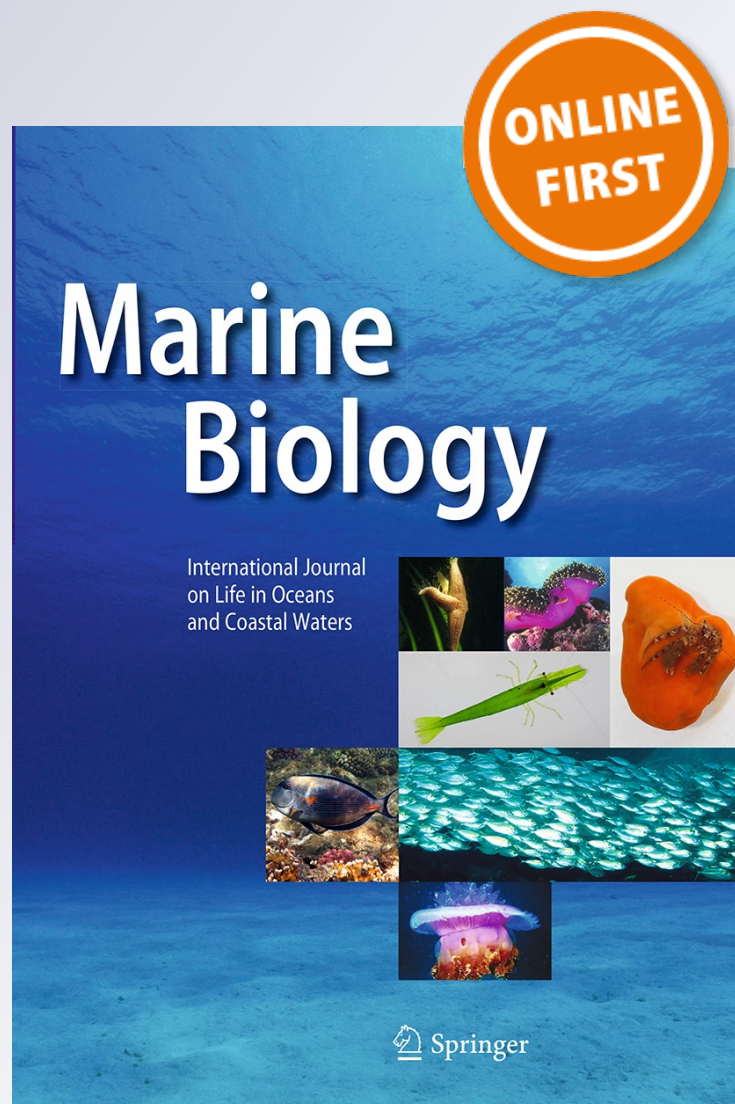B. Louise Chilvers & Martin Krkošek

ONLINE FIRST

Marine Biology

International Journal
on Life in Oceans
and Coastal Waters

Springer

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ORIGINAL PAPER

Population dynamics reveal conservation priorities of the threatened New Zealand sea lion *Phocarctos hookeri*

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Abstract Understanding the life history basis of the population dynamics of threatened species is crucial to their assessment and recovery. Within the Southern Pacific Ocean, the decline and range contraction of New Zealand sea lions (NZSLs) (*Phocarctos hookeri*) are an exemplary case of a major fisheries and conservation controversy. Despite the use of bycatch reduction measures, the main population of the NZSL has declined since 1998 and its vulnerability to threats is poorly understood. Here we develop a population model for the declining population of the endangered NZSL at the Auckland Islands, New Zealand ($50°30'$S, $166°17'$E), parameterised by mark-recapture data of 2928 female NZSLs spanning 15 years from 1998 to 2012, and provide the first comprehensive analysis of NZSL population dynamics and its relationship to life history. Our model closely predicts the observed trend in population censuses of the main breeding population. We found that the population will continue to decline without effective intervention. Furthermore, we found that the population growth rate is most responsive to changes in survival of adult female NZSLs—the demographic group that is most threatened by fishery bycatch. Nevertheless, inferences about the efficacy of NZSL bycatch reduction measures are still imprecise. Combined, this could explain why the main population of NZSLs continues to decline. Our results emphasise that reliable data on bycatch reduction measures are needed, if they are to be shown to protect key demographic groups of marine mammals.

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Introduction

The loss of marine top predators is a global challenge for ecosystem conservation (Parsons et al. 2014). However, conservation actions are often implemented without assessing their efficacy to avoid population declines and sparse data make the assessment of threat reduction measures difficult (Cox et al. 2007; Lewison et al. 2004; Martin et al. 2014; Thorpe and Stanley 2014). In this regard, an understanding of the life history basis of population dynamics is a key component in assessing the vulnerability of a species to threats and the efficacy of conservation actions (Lewison et al. 2013). Unfortunately, a missing link between conservation actions and the basic life history of the focal species is common in threatened species management (Kissel et al. 2014; Martin et al. 2014).

New Zealand (NZ) is a hot spot of marine mammal biodiversity (Schipper et al. 2008), but with 56 marine mammals considered threatened (Baker et al. 2010). The New Zealand sea lion (NZSL) (*Phocarctos hookeri*) is NZ's only endemic pinniped (Baker et al. 2010) and has

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one of the smallest population estimates for any otariid (Childerhouse and Gales 1998). The NZSL is listed as 'endangered' by the International Union for Conservation of Nature (Chilvers 2015) and 'nationally critical' under the NZ threat classification system (Baker et al. 2010). Whilst the mainland colony was extirpated c. 730 years ago (Wilmhurst et al. 2008), there still exists a separate genetic lineage (Collins et al. 2014) on NZ's sub-Antarctic offshore islands (Childerhouse and Gales 1998), where 73 and 27 % of the annual pup production takes place at Auckland Islands and Campbell Islands, respectively (Maloney et al. 2012). The restricted range makes the NZSL vulnerable to catastrophic events, which highlights the importance of protecting the remaining colonies (Department of Conservation 2009).

Since 1998, the NZSL population at the Auckland Islands has declined by approximately 50 % (Robertson and Chilvers 2011). There are several hypotheses for the population decline, including bacterial diseases of pups (Castinel et al. 2007a, b), bycatch mortality of adult NZSLs and resource competition with commercial fisheries operations in New Zealand waters (Chilvers et al. 2005; Meynier et al. 2009; Robertson and Chilvers 2011; Wilkinson et al. 2003). The latter two hypotheses are linked to the temporal and spatial overlap of lactating female NZSLs in primary foraging waters with commercial trawl fisheries that harvest key prey species [e.g. arrow squid (*Nototodarus sloanii*)] and catch NZSLs as bycatch (Chilvers et al. 2011; Wilkinson et al. 2003). Although bycatch reduction measures have been consistently used in the commercial fisheries since 2005 (Hamilton and Baker 2015), the NZSL population decline has continued (Chilvers 2012b). Therefore, the impact of these threats and the efficacy of conservation actions remain unclear (Robertson and Chilvers 2011) and several population models have produced conflicting results about the effect of epidemics and fisheries bycatch on the NZSL population (e.g. Breen et al. 2003; Chilvers and MacKenzie 2010; Chilvers 2012b; Hamilton and Baker 2014; Roberts and Doonan 2014). However, no previous NZSL study has scrutinised the response of the population growth rate to threats and possible conservation actions, particularly in the context of quantified stochastic effects (i.e. observational error and process noise such as environmental variability) in focal demographic parameters.

Stochastic effects that contribute to observed population dynamics are known to be crucial factors that influence our ability to detect population declines (e.g. Connors et al. 2014). Nevertheless, these have not been rigorously accounted for in mark-recapture analyses, including NZSLs, because of its impractical implementation within a frequentist framework (Tenan et al. 2014). However, the quantification of environmental variability can increase our understanding of processes that could cause a population decline (Melbourne and Hastings 2008). In this regard, stochastic population models are reliable for detecting a population decline (Oppel et al. 2014) and to measure the proportional change of the population growth rate in response to changes in demographic parameters with an elasticity analysis (Benton and Grant 1999; Caswell 2001).

In this study, we use a 15-year data set of 2928 female NZSLs to: (1) develop and implement a multistate state-space Cormack–Jolly–Seber (CJS) model (Gimenez et al. 2007) with random time effects; (2) develop and parameterise a matrix population model; (3) estimate the asymptotic population growth rate; (4) confirm the deterministic trend via temporal stochastic population projections and (5) identify key demographic parameters for NZSL management via an elasticity analysis. (6) We validate the model predictions against independent census data for NZSL pups.

Materials and methods

Study population

We analysed open access data (Department of Conservation 2014) consisting of 2928 mark-recapture histories for female NZSLs that were double tagged as pups on Sandy Bay (50°30′S, 166°17′E), spanning the breeding seasons of 1998 to 2012. This population accounts for approximately 16 % of the total pup production of NZSLs and is the second largest colony at the Auckland Islands (Chilvers 2010). Data were collected from 1 December until 20 February in the subsequent year (Chilvers and MacKenzie 2010), such that all pups were born (mean pup birth date 26 December) before the end of a sampling season (Chilvers et al. 2007b, a). Hereafter, breeding seasons are referred to the January year (i.e. the 1997/1998 season is referred to as 1998). Possible erroneous sex determinations during the first three years of a sea lion's life were updated using subsequent recaptures, when the individual's sex was identified with high confidence (Chilvers, pers comm).

Analysis of population dynamics

The NZSL is a polygamous species (Chilvers 2012b), hence we assumed that population dynamics are limited by female demographic parameters. Therefore, we described population dynamics of female NZSLs using a stage-classified matrix population model (Caswell 2001) with five population stages: (1) pup (0 years), (2) juvenile (2–3 years). At age 4, females either produce a pup

or delay reproduction (Childerhouse et al. 2010). After a breeding event, an individual can either reproduce again or skip breeding for consecutive seasons (Chilvers et al. 2009). Therefore, we partitioned adults (4+ years) into (3) adult & delayed breeding, (4) adult & breeding and (5) adult & skipped breeding. An adult individual was considered a first-time breeder based on the time it was first recorded nursing a pup. The model can be described as follows:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t \tag{1}$$

with $\mathbf{n}_t$ and $\mathbf{n}_{t+1}$, the population vector providing the number of individuals in stages 1 to 5 at time t and $t+1$ respectively, and population projection matrix $\mathbf{A}$:

$$\mathbf{A} = \begin{pmatrix} 0 & \overline{\phi}_2\overline{\psi}_{24}0.5 & \overline{\phi}_{\mathbf{3,4,5}}\overline{\psi}_{34}0.5 & \overline{\phi}_{\mathbf{3,4,5}}(1-\overline{\psi}_{45})0.5 & \overline{\phi}_{\mathbf{3,4,5}}\overline{\psi}_{54}0.5 \\ \overline{\phi}_1 & \overline{\phi}_2(1-\overline{\psi}_{23}-\overline{\psi}_{24}) & 0 & 0 & 0 \\ 0 & \overline{\phi}_2\overline{\psi}_{23} & \overline{\phi}_{\mathbf{3,4,5}}(1-\overline{\psi}_{34}) & 0 & 0 \\ 0 & \overline{\phi}_2\overline{\psi}_{24} & \overline{\phi}_{\mathbf{3,4,5}}\overline{\psi}_{34} & \overline{\phi}_{\mathbf{3,4,5}}(1-\overline{\psi}_{45}) & \overline{\phi}_{\mathbf{3,4,5}}\overline{\psi}_{54} \\ 0 & 0 & 0 & \overline{\phi}_{\mathbf{3,4,5}}\overline{\psi}_{45} & \overline{\phi}_{\mathbf{3,4,5}}(1-\overline{\psi}_{54}) \end{pmatrix} \tag{2}$$

which corresponds to the life cycle graph in Fig. 1. The projection interval is one year. Diagonal matrix entries reflect individuals that remain within stage k, whereas sub-diagonal entries and the final entry in row four denote transitions into any other life history stage (Table 1). $\overline{\phi}_{3,4,5}$ denotes constant adult survival for the adult breeding states, which are indicated by bold letters within each subscript. The top row of matrix $\mathbf{A}$ allows the contribution of pups by stages 2 to 5 as follows: NZSL births are highly synchronised (Chilvers et al. 2007a) and most pups are born before the 2nd of January (Chilvers et al. 2007a), whereas recaptures and the breeding status were recorded until 20 February (Chilvers and MacKenzie
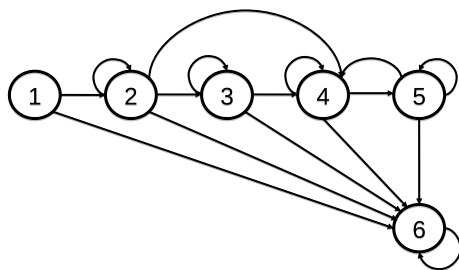
2010). Therefore, $\mathbf{A}$ reflects a birth-pulse population that was sampled via a post-breeding census (Caswell 2001). In this regard, the first row represents stage-specific contributions of pups after transitioning into or remaining in stage 4. Female NZSL pups are produced with a sex ratio of 0.5 (Chilvers 2012c).

To estimate female demographic parameters for NZSLs, we modified an age-structured mark-recapture model from Chilvers and MacKenzie (2010) using the stage structure of population projection matrix $\mathbf{A}$. We pooled individuals between 1–3 years, because the data are not sufficient to estimate survival for each age separately and these stages are all pre-reproductive. We parameterised our demographic model based on the most parsimonious model of a preliminary model selection (Online Resource A). The model treated adult survival as independent of the breeding status; however, adult female recapture differed between non-breeding (stages 3 and 5) and breeding (stage 4) adults.

We modelled tag loss for double-tagged pups and older individuals, to avoid underestimation of survival (Chilvers

Table 1 Parameter description of the CJS and matrix population model for female NZSLs

Parameter	Description
$\overline{\phi}_1$	Mean pup survival
$\overline{\phi}_2$	Mean juvenile survival
$\overline{\phi}_{3,4,5}$	Mean adult survival
$\sigma^2_{\mathrm{logit}(\phi_{1,t})}$	Temporal variance of pup survival (on logit scale)
$\sigma^2_{\mathrm{logit}(\phi_{2,3,4,5,t})}$	Temporal variance of juvenile and adult survival (on logit scale)
$\overline{p}_2$	Mean juvenile recapture
$\overline{p}_{3,5}$	Mean adult non-breeder recapture
$\overline{p}_4$	Mean adult breeder recapture
$\overline{\psi}_{23}$	Mean transition from 'juvenile' to 'adult & delayed breeding'
$\overline{\psi}_{24}$	Mean transition from 'juvenile' to 'adult & breeding'
$\overline{\psi}_{34}$	Mean transition from 'adult & delayed breeding' to 'adult & breeding'
$\overline{\psi}_{45}$	Mean transition from 'adult & breeding' to 'adult & skipped breeding'
$\overline{\psi}_{54}$	Mean transition from 'adult & skipped breeding' to 'adult & breeding'
$\overline{q}_1$	Mean tag loss for pups
$\overline{q}_{2+}$	Mean tag loss for 1+ years individuals

Fig. 1 Life cycle graph of female New Zealand sea lions. Numbers describe the following stages: *1* pup (0 years), *2* juvenile (1–3 years), *3* adult and delayed breeding (4+ years), *4* adult and breeding (4+ years), *5* adult and skipped breeding (5+ years), *6* dead. *Arrows* indicate a possible stage transition from one year to the next. Arrows to stage 6 are mortalities. The corresponding state process matrix *Ω* used for parameter estimation, including the tag loss process, can be found in Table B1 (Online Resource B)

and MacKenzie 2010). We considered tag loss, the probability a single tag is lost per year is $\overline{q}_1$ for pups and $\overline{q}_{2+}$ if older. Simultaneous tag loss was modelled as $\overline{q}_1^2$ and $\overline{q}_{2+}^2$. Individuals with 0 retained tags were treated as a latent state.

We estimated model parameters with the multistate state-space formulation of the CJS model (Gimenez et al. 2007). The product of life history-specific survival, transitions and tag loss (Table 1) was implemented in a multistate process by:

$$z_{i,t+1}|z_{i,t} \sim \text{categorical}(\Omega_{z_t,1\ldots S,t}) \qquad (3)$$

with the categorical distribution-based likelihood that individual i is in state z the next year given its current state. Ω is a three-dimensional matrix with the first and second dimensions denoting the state of departure and arrival, respectively, each with length $S = 14$ possible states (Table B1 (Online Resource B)). In addition, we modelled a third dimension with length 15 (years), where survival was allowed to vary in response to random time effects. These were modelled via $\sigma_{\text{logit}(\phi_{k,t})}^2$, the temporal variance of survival on the logit scale to ensure an estimated interval between [0, 1].

The observation process, which is dependent on recapture probabilities (Table 1), is described by:

$$y_{i,t}|z_{i,t} \sim \text{categorical}(\Theta_{z,1\ldots O}) \qquad (4)$$

where $y_{i,t}$ is the state an individual was seen during the recapture event given it is in state z. Θ is a two-dimensional matrix with the actual state on the first and the observed state on the second dimension with length $O = 9$ (Table B2 (Online Resource B)). Individuals without retained tags and dead individuals were treated as not observable. The 2.5th and 97.5th percentiles of the estimated posterior distributions and post-processed results were taken as 95 % credible intervals (CrI).

Uniform prior distributions ($U(0, 1)$) were provided for probabilities. Because multiple transitions exist for juveniles, we applied a multinomial link function and specified normal priors on logit scale for $\overline{\psi}_{23}$ and $\overline{\psi}_{24}$ to ensure an estimated interval within [0, 1]. We found no sensitivity of estimates on priors by comparing model runs with alternative prior ranges ($N(0, 0001)$, $N(0, 001)$). Furthermore, uniform prior distributions were provided for temporal standard deviations of survival on the logit scale $\sigma_{\text{logit}(\phi_{k,t})}$ (Gelman 2006). In that case, there existed a considerable overlap between the estimated posterior and supplied prior distribution for $\sigma_{\text{logit}(\phi_{2,t})}$. Therefore, we decided to specify equal random effects for juveniles and adults. This parameterisation had no effect on other model parameter estimates (Online Resource C1 and C2). Finally, we found no sensitivity of parameter estimates when supplying alternative prior ranges ($U(0, 5)$, $U(0, 10)$) for temporal standard deviations.

We estimated the asymptotic population growth rate λ ($\lambda > 1$: increase, $\lambda < 1$: decrease) by calculating the eigenvalue of the deterministic projection matrix **A**. Moreover, we derived the proportional response of λ to changes in demographic parameters ($\overline{\phi}_k$, $\overline{\psi}_{kl}$) by conducting an elasticity analysis on the product of matrix entries and deriving the lower-level elasticities via their chain product (Caswell 2001). The elasticities for survival were used to calculate the required proportional increase in survival in order to stop the population decline (Caswell 2001), i.e. $\lambda = 1$. Elasticities reflect the response of the population growth rate in response to a single parameter change, whilst other parameters are assumed to be fixed (Caswell 2001). To additionally explore the effect of combined changes in pup and adult survival, we computed the population growth rate for all possible combinations of pup and adult survival (range 0.01 to 0.99, steps 0.01) with respect to posterior samples of all remaining model parameters (i.e. juvenile survival and transition probabilities). For each combination, we quantified the proportion of posterior density of λ smaller than, equal to, or larger than 1 using numerical integration.

Furthermore, we simulated temporal stochastic population projections starting in 1998, making each entry of **A** a linear function of time using temporal stochastic samples of survival with logit mean survival and the corresponding temporal variance that was estimated with the CJS model. The initial population vector was derived from the censused number of female pups at the Auckland Islands in 1998 (Chilvers 2010), and the stable stage distribution **w** given by the deterministic projection matrix. We projected the population size for all female NZSLs at the Auckland Islands. For model validation, we compared the number of projected female pups with an independently censused number of female NZSL pups (sex ratio = 0.5) at the Auckland Islands between 1998 and 2014 (Childerhouse 2014; Chilvers 2010).

Analyses were performed in the statistical programme *R* (v2.14.0; Development Core Team 2011). The multistate state-space CJS model was written in *JAGS* (v 3.3.0; Plummer 2003) using the *R*-package *R2JAGS* (v 0.03-08; Su and Yajima 2012). Parallel computation was carried out using the *R*-package *dclone* (Sólymos 2010). All post-processing was conducted using the *CODA* package (Plummer et al. 2006).

Results

Model validation

Our model closely predicted the actual population trend of NZSLs at the Auckland Islands given the close match
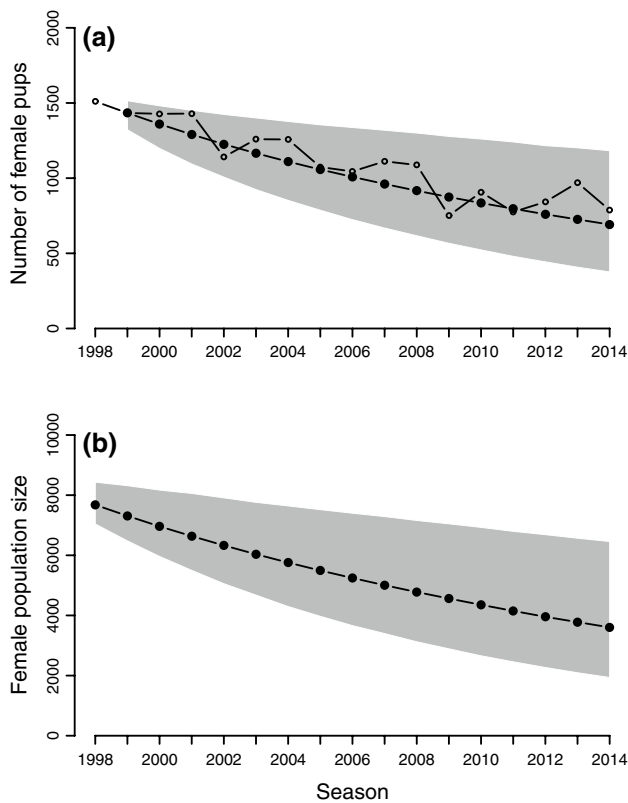
Fig. 2 Population projections. **a** Female pups: *filled circles*: median female pup number in year *t*, *open circles*: the censused number of female pups from Chilvers (2010) and Childerhouse (2014); **b** female population size: *filled circles*: median female NZSL number in year *t*. *Grey area*: 95 % credible interval

Table 2 Parameter estimates from the CJS model for female NZSLs

Parameter	Median	95 % Credible interval	
		2.5 %	97.5 %
$\overline{\phi}_1$	0.185	0.121	0.265
$\overline{\phi}_2$	0.978	0.955	0.996
$\overline{\phi}_{3,4,5}$	0.883	0.853	0.911
$\sigma^2_{\text{logit}(\phi_{1,t})}$	0.673	0.266	2.024
$\sigma^2_{\text{logit}(\phi_{2,3,4,5,t})}$	0.023	0.00006	0.336
$\overline{p}_2$	0.189	0.170	0.210
$\overline{p}_{3,5}$	0.836	0.791	0.878
$\overline{p}_4$	0.963	0.926	0.995
$\overline{\psi}_{23}$	0.225	0.203	0.249
$\overline{\psi}_{24}$	0.012	0.007	0.018
$\overline{\psi}_{34}$	0.405	0.364	0.449
$\overline{\psi}_{45}$	0.293	0.248	0.342
$\overline{\psi}_{54}$	0.769	0.673	0.852
$\overline{q}_1$	0.153	0.096	0.222
$\overline{q}_{2+}$	0.121	0.106	0.142

Posterior distributions are shown in Online Resource C2

between the median annual number of female pups and the corresponding female pup census (Fig. 2a).

Female NZSL demographic parameters

Table 2 shows that survival differed significantly between pups, juveniles and adult NZSLs and was lowest for pups. Furthermore, the estimate for the temporal variance of pup survival indicates considerable variation of pup survival, between 1998 and 2012, compared to the low temporal variance of adult survival. The estimated transition rates reflect that many adults first delay breeding (stage 3). Moreover, there exists only a probability of 0.405 (95 % CrI 0.364–0.449) to leave stage 3. However, once the first breeding event occurred, the probability of recent breeders to delay the next breeding event was only 0.293 (95 % CrI 0.248–0.342) and 0.769 (95 % CrI 0.673–0.852) to breed again after skipping breeding. We found that tag loss was high for both pups (stage 1) and older individuals (stages 2, 3, 4 and 5). The estimated recapture for adult individuals was high and differed significantly between non-breeding and breeding adults. However, recapture of juveniles was low.

Analysis of population dynamics

The population projection matrix **A** yielded a significant negative asymptotic population growth rate of 0.950 (95 % CrI 0.920–0.978) per year. This deterministic pattern is underpinned by Fig. 2b, which shows that the population declined between 1998 and 2012 (the sampling period) even if environmental variability and observational error are taken into account. Assuming that the environmental conditions continued after that period, we further simulated the most recent breeding seasons and found that the female population size in 2014 measures approximately 4000 individuals.

The results of our elasticity analysis show that the population growth rate only responds to very large changes in transitions between breeding states (Table 3). It is also evident from the derived elasticity of pup survival [0.048 (95 % CrI 0.038–0.058)] that changes in pup survival have relatively limited impact on the population growth rate (Table 3). For example, to stop the population decline, it is required to increase the current pup survival of 0.185 (95 % CrI 0.121–0.265) to 0.388 (95 % CrI 0.290–0.493). In contrast, the elasticity of adult survival, given as the sum of elasticities for stages 3, 4 and 5 [0.680 (95 % CrI 0.612–0.745)], indicates that changing adult survival can lead to a large response in the population growth rate. In other words, an increase in the recent adult survival from 0.883 (95 % CrI 0.853–0.911) to 0.953 (95 % CrI 0.929–0.973) is required to stop the population decline. Moreover, the

Table 3 Lower-level elasticity (e_x) of demographic parameter x

Parameter	Median	Credible interval	
		2.5 %	97.5 %
$e_{\overline{\phi}_1}$	0.048	0.038	0.058
$e_{\overline{\phi}_2}$	0.276	0.218	0.336
$e_{\overline{\phi}_{3,4,5}}$	0.097	0.079	0.114
$e_{\overline{\phi}_{3,4,5}}$	0.431	0.375	0.491
$e_{\overline{\phi}_{3,4,5}}$	0.150	0.117	0.186
$e_{\overline{\psi}_{23}}$	−0.007	−0.016	0.0004
$e_{\overline{\psi}_{24}}$	−0.0001	−0.0007	0.0002
$e_{\overline{\psi}_{34}}$	0.003	0.002	0.004
$e_{\overline{\psi}_{45}}$	0.0007	−0.0004	0.002
$e_{\overline{\psi}_{54}}$	−0.0006	−0.002	0.0004

Bold letters indicate elasticity of adult survival in stages 3, 4 or 5
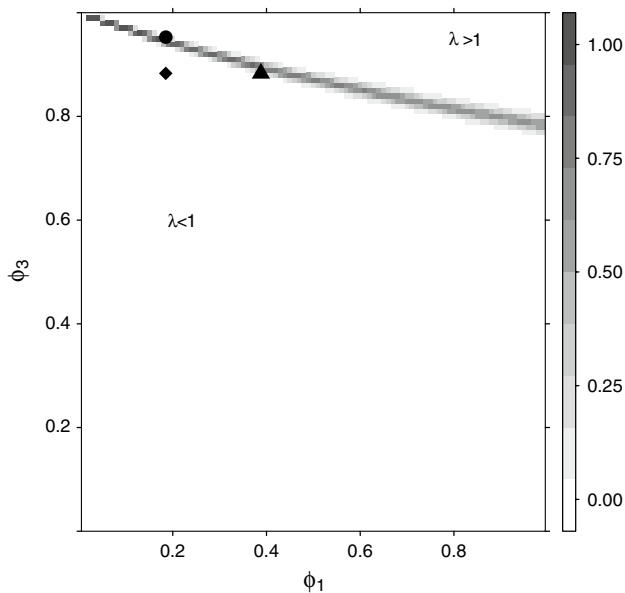

Fig. 3 Predicted population growth rate (λ) for combined changes of pup (ϕ_1) and adult ($\phi_{3,4,5}$) survival. Shown are the proportion (between 0 and 1) of posterior density for λ which equals to 1 and thus represents a stable population (*grey-scale area*). Combination of ϕ_1 and $\phi_{3,4,5}$ that cause a declining population ($\lambda < 1$) are below the *grey-scale area* and above if leading to an increasing population ($\lambda > 1$). For comparison, the symbols locate the median-combined survival probabilities estimated from the data (*diamond*), given the sole improvement of adult survival (*dot*) or pup survival (*triangle*) as suggested by elasticity analysis

highest elasticity for adult survival in stage 4 [0.431 (95 % CrI 0.375–0.491)] shows that the population growth rate is most responsive to changes in adult survival for breeding female NZSLs.

When comparing combined changes of pup and adult survival, we found that a stable or increasing population ($\lambda \geq 1$) is theoretically possible for all values of pup survival between 0.01 and 0.99, if compensated through a corresponding adult survival probability but not *vice versa* (Fig. 3). For example, it was still possible to compensate low pup survival of 0.10 using an adult survival probability of 0.97 (in that case, almost 100 % of posterior samples for λ equal to 1). In contrast, there existed no pup survival probability that generated $\lambda \geq 1$ if adult survival was smaller than 0.77. Furthermore, increasing adult survival led to more reliable predictions of improved population growth in comparison with increased pup survival. For example, improving adult survival to 0.95 (according to elasticity analysis) produced posterior samples for λ whose density was distributed as followed: 1 % was smaller than 1, 48 % was equal to 1 and 51 % was larger than 1. In contrast, improving pup survival to 0.39 produced posterior samples for λ whose density included still values that reflect population decline (below 1: 38 %, equal to 1: 61 %, larger than 1: 1 %). Simultaneous increases in pup and adult survival had additive effects such that less improvement of each survival probability was required compared to a single parameter change. For example, with improved pup survival of 0.30, only an adult survival of 0.92, compared to 0.95, would have been required to predict a posterior sample density for λ that was mainly larger than or equal to one (below 1: 7 %, equal to 1: 73 %, larger than 1: 26 %).

Discussion

Our study confirms a significant negative population growth rate of NZSLs. The conducted elasticity analysis produced results that corroborate the findings of previous works in large vertebrate life history (e.g. Eberhardt 2002) and reflect the vulnerability of a threatened marine mammal to adult mortality caused by commercial fisheries. Nevertheless, our results are in conflict with current studies that highlight reduced pup survival and adult reproduction as the key factors for the NZSL population decline (Hamilton and Baker 2014; Roberts and Doonan 2014).

Previously conducted demographic studies on NZSLs heavily relied on demographic information based on other pinniped species (Chilvers 2012a; Hamilton and Baker 2014) or identified relationships between demographic parameters and factors, without quantifying how much these contributed to the observed biological variation (Roberts and Doonan 2014). Moreover, neither of these approaches has assessed the effect of observational error on model outcomes. In contrast, we disentangled environmental variability from observational error by modelling temporal changes of survival via random effects. We therefore provide a fundament for further demographic modelling to assess the impact of threats on the population of NZSLs.

Roberts and Doonan (2014) state that the population decline might be linked to a decrease in first- or second-year survival. We found that both, survival of female pups [0.185 (95 % CrI 0.121–0.265)] and adult female NZSLs [0.883 (95 % CrI 0.853–0.911)] were low compared to other species. For example, survival probabilities for Steller sea lions (*Eumetopias jubatus*) were estimated to be 0.719 and 0.941 for pups and adults, respectively (Fritz et al. 2014). The only pinniped species with comparable pup survival to NZSLs is the crabeater seal (*Lobodon carcinophaga*) (0.21) (Mills 2012). Nevertheless, the crabeater seal is recognised as the most abundant seal species (Southwel 2008). This demonstrates that neonatal survival is a minor determinant for the population growth rate of long-lived mammals (Heppel et al. 2000). Moreover, this accords with our results, which show that the population growth rate of female NZSLs is relatively unresponsive to changes in pup survival but strongly responds to a shift in adult survival. We have not modelled temporal changes in transitions of breeding states. However, the median probability to breed again $(1 - \psi_{45})$ [0.707 (95 % CrI 0.658–0.752)] and to resume reproduction after skipping breeding for one, or consecutive, seasons [0.769 (95 % CrI 0.673–0.852)] was high and the low elasticities for breeding-state transitions suggest that only large changes in these transitions will have a strong effect on the population growth rate.

The estimates for the temporal variance of survival reflect high temporal variability of pup survival, but that adult survival remained relatively constant throughout the study period. Thus, our results are in accordance with the demographic buffering hypothesis, which suggests that the population growth rate of long-lived mammals is buffered against environmental fluctuations by affecting only the less important life history parameters (i.e. survival of younger individuals and adult reproduction) (e.g. Rotella et al. 2012). Consequently, the low survival rate of adult female NZSLs is unlikely to be the result of short-term environmental fluctuation rather than some anthropogenic threat. It has been hypothesised that bycatch mortality has affected NZSLs prior to the introduction of sea lion exclusion devices (SLEDs)—a bycatch mitigation measure designed to allow the release of non-targeted NZSLs (Chilvers 2008; Werner et al. 2006)—and they may currently be threatened by resource depletion (Chilvers 2008; Robertson and Chilvers 2011). Considering the strong impact of changes in adult survival on the population growth of NZSLs, these threats and their mitigation need to be assessed with great care.

The elasticity analysis is often criticised, because it neither accounts for a realistic range in focal parameters nor for the ability to manage the identified key parameter (Norris 2004). However, the high elasticity for adult survival provides a good sense of the importance of precise and accurate knowledge on SLED efficacy. Across the Auckland Islands shelf, a range of 15 (95 % CI 5–29) to 194 (95 % CI 100–356) NZSLs interacted with trawl nets between 1996 and 2011 (Thompson et al. 2013). Studies on the survival likelihood of bycaught NZSLs (for a review see Hamilton and Baker 2015) have not quantified how many dead NZSLs fall out of the trawl net through SLEDs nor are numbers of individuals known that die (e.g. through head injuries) after escaping a trawl net (Robertson 2015 in press). Compared to that high uncertainty in SLED efficacy, we found that a relatively small increase in adult survival (on average 7 %) would be enough to stop the population decline. Moreover, the effect of improved adult survival would be higher than we were able to quantify because we have not accounted for the additional survival of one pup per breeding female due to the mother-pup bond reported for NZSLs (Augé et al. 2009). Therefore, we suggest that a precautionary approach to SLED efficacy for NZSLs should be taken.

In contrast, to stop the population decline, we require a large increase in pup survival (on average by 20.3 %), which probably involves the intervention into naturally occurring processes. For example, trauma, caused through injuries of fighting bulls within the harem, is identified as the main reason of NZSL pup mortality during the first three months (Castinel et al. 2007a), and is relatively common within pinniped populations (Le Boeuf and Campagna 1994). The second most important cause of NZSL pup mortality during the first three months is bacterial infections that caused three epidemics at the Auckland Islands since 1998 (Castinel et al. 2007a; Chilvers et al. 2007a). Although epidemics could pose a threat to small populations (Young 1994), other pinniped populations have recovered after mass mortality events (e.g. Reijnders et al. 1997). Furthermore, the intervention into host–pathogen dynamics (e.g. vaccination) is not without risks for the host species, and most attempts on wildlife populations have been only partially successful (Breed et al. 2009). The low elasticity of pup survival suggests that the response of the NZSL population provides an undesirable compromise between the uncertain outcome and the risks of disease management.

It is possible that management actions with a focus on one population parameter, such as pup survival, would be beneficial for outcomes of actions to improve survival of another demographic group (e.g. adults). Our exploration of combined changes demonstrated that less improvement for adult survival is required if actions can simultaneously ensure improved pup survival. Nevertheless, the most reliable predictions of the population growth rate were caused through altered adult survival. Furthermore, population equilibrium was still possible under extreme low pup survival (e.g. 0.10) if compensated through high adult survival but not *vice versa*, which underpins the buffering function of adult survival in marine mammals

against high mortality in earlier stages (Rotella et al. 2012). Ensuring that adult survival maintains this buffering function is therefore paramount in marine mammal conservation.

The high elasticity for adult survival emphasises the need for a precise and accurate estimate for this parameter. A known source of bias in mark-recapture studies is the non-consideration of the loss of markings (Oosthuizen et al. 2010). Our estimates for tag loss were relatively high and in accordance with estimates by Chilvers and MacKenzie (2010). Moreover, all adult NZSLs had a high recapture probability. In particular, breeding sea lions were recaptured nearly 100 %, which reflects that breeding females regularly return to their dependent pup. Consequently, we assume only a small bias of tag loss and misidentifications of first-time breeders. In contrast, juvenile individuals were often overlooked, as suggested by their low recapture probability. One possible explanation could be that juveniles move to other areas before starting to reproduce. However, the high philopatry of NZSLs does not suggest that emigration is apparent in the NZSL population at the Auckland Islands (Chilvers and Wilkinson 2008). For example, Chilvers and Wilkinson (2008) found that only 0.5 % of 293 female NZSLs that were studied at Sandy Bay, between 1990 and 2001, have bred at a nonnatal site. Finally, the validation of our temporal stochastic model predictions against an independent pup census suggests that we recovered sufficiently the real population dynamics and that possible above-mentioned biases are likely to be small.

The elasticity analysis is used to determine the change in the population growth rate in response to changes of average demographic rates (Caswell 2001). Amongst pinnipeds, the NZSL has one of the smallest and most range-contracted populations (Childerhouse and Gales 1998) and our results suggested continued population decline. Small populations can suffer from low genetic diversity (Frankham 1996), which might be even more prevalent in polygynous mating systems (Nunney 1993). Random events, such as epidemics, can further reduce beneficial alleles just by chance (genetic drift) and thus accelerate the predicted population decline (Lande 1994). However, genetic diversity in NZSLs does not appear to be smaller compared to that of other pinniped species (Robertson and Chilvers 2011). Alternatively, demographic stochasticity, the randomness in the fate of single animals can lead to smaller population growth as expected under average survival (Lande 1993) and might occur before genetic effects drive population extinction (Wootton and Pfister 2013). Considering the small population size that the NZSL population is currently approaching, it might be of interest to explore the robustness of elasticity patterns against genetic effects and demographic stochasticity. Despite that, there exists indication that management based on elasticities of λ is robust even if several biological processes, such as demographic stochasticity, are not considered (Caswell 2001).

The conservation of marine top predators is challenging, because it works at the intersection between conservation management and ecology (Brussard 1991). To avert species extinction, effective solutions are required (Martin et al. 2014). The history of the NZSL provides an exemplary case where management actions are implemented without quantifying the population's vulnerability to a threat. Our results highlight the importance of basic life history analysis for marine mammal conservation, particularly when the level of knowledge about human-induced mortality is low.

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